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Endocranial volumes of primate species: Scaling analyses using a comprehensive and reliable dataset

Karin Isler[1], E. Christopher Kirk[2], Joseph M. A. Miller[3], Gene A. Albrecht[4], Bruce R. Gelvin[5] and Robert D. Martin[6]

1) Anthropological Institute and Museum, University of Zürich-Irchel, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

2) Department of Anthropology, University of Texas at Austin, 1 University Station C3200, Austin, TX 78712, USA.

3) Division of Integrative Anatomy, Department of Pathology & Lab Medicine, UCLA Geffen School of Medicine, Los Angeles, CA 90095, USA.

4) Department of Cell and Neurobiology, Keck School of Medicine, University of Southern California, Los Angeles, CA 90033, USA.

5) Department of Anthropology, California State University at Northridge, Northridge, CA 91330, USA. (Professor Emeritus).

6) Department of Anthropology, The Field Museum, 1400 S. Lake Shore Drive, Chicago, IL 60605-2496, USA.

Corresponding author: Karin Isler, Anthropological Institute and Museum, University of Zürich-Irchel, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland. E-mail: kisler@aim.uzh.ch, Fax ++41 44 635 68 04.

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Abstract

We present a compilation of endocranial volumes (ECV) for 176 non-human primate species, based on individual data collected from 3813 museum specimens, at least 88% being wild-caught. In combination with body mass data from wild individuals, strong correlations between endocranial volume and body mass within taxonomic groups were found. Errors attributable to different techniques for measuring cranial capacity were negligible and unbiased. The overall slopes for regressions of log ECV on log body mass in primates are 0.773 for least-squares regression and 0.793 for reduced major axis regression. The least-squares slope is reduced to 0.565 when independent contrasts are substituted for species means (branch lengths from molecular studies). A common slope of 0.646 is obtained with logged species means when grade shifts between major groups are taken into account using ANCOVA. In addition to providing a comprehensive and reliable database for comparative analyses of primate brain size, we show that the scaling relationship between brain mass and ECV does not differ significantly from isometry in primates. We also demonstrate that ECV does not differ substantially between captive and wild samples of the same species. ECV may be a more reliable indicator of brain size than brain mass, because considerably larger samples can be collected to better represent the full range of intraspecific variation. We also provide support for the maternal energy hypothesis by showing that BMR and gestation period are both positively correlated with brain size in primates, after controlling for the influence of body mass and potential effects of phylogenetic relatedness.

Introduction

Comparative studies of brain evolution continue to be a major focus of interest in biological anthropology. Various lines of evidence suggest that brain size in primates is both

correlated with cognitive abilities (Reader and Laland, 2002; Deaner et al., 2007) and influenced by a variety of social, ecological, and physiological variables (Clutton-Brock and Harvey, 1980; Byrne and Whiten, 1988; Sawaguchi, 1990; Aiello and Wheeler, 1995; Martin, 1996). The scaling relationship between brain size and body mass in primates (and mammals generally) has also been a major topic of debate, in part because the influence of body mass must be considered in comparative analyses of brain evolution (e.g. Jerison, 1973; Martin, 1981; Hofman, 1989; Allman, 1999). However, a thorough understanding of brain-body allometry is impeded by numerous factors (reviewed in Deacon, 1990), including grade differences between primate clades. As many authors have noted, the slopes of best-fit lines for brain mass against body mass tend to be higher in analyses of more inclusive taxa (e.g., orders and suborders) and lower in analyses of less inclusive taxa (families, subfamilies, and genera, e.g. Martin and Harvey, 1985). Furthermore, the largest living primates (all catarrhines) tend to have relatively large brains, so allometric adjustments applied across primates with a single best-fit line tend to underestimate relative brain size in large taxa such as baboons and apes.

Additional controversy has arisen over the most appropriate techniques to control for potential phylogenetic effects in analyses of brain evolution. Many authors have employed statistical methods designed to take the influence of phylogenetic relatedness into account (e.g., Felsenstein's (1985) method of independent contrasts). It has been claimed that these methods "remove" grade shift effects (following Harvey and Pagel, 1991), but there is a major drawback in their built-in tendency to magnify the effects of "error" variation (e.g. Ricklefs and Starck, 1996; Martin et al., 2005). In a large sample, calculating contrasts between closely related species may yield a bias towards a lower slope of the best-fit line, because contrasts within genera or within subfamilies predominate.

One important limitation of previous research into primate brain evolution has been sample quality (reviewed in Healy and Rowe, 2007). Most authors have relied either on brain mass data derived from very small samples (e.g., Bauchot and Stephan, 1966, 1969; Stephan et al., 1970; Stephan et al., 1981) or on endocranial volume data from compilations without specification of sample size or sex (e.g., Clutton-Brock and Harvey, 1980). Moreover, many former subspecies are now recognized as full species. Such changes in alpha taxonomy could have an impact on comparative analyses, particularly when newly recognized sister species differ markedly in body size. In sum, unnecessarily large error variation has in the past complicated the interpretation of comparative studies of brain size evolution in primates. Some authors have also augmented available species data through duplication of brain mass values between species without explicitly noting the fact (e.g. Snodgrass et al., 2007). In addition, it may sometimes be preferable to include only female data in comparative analyses, particularly in the context of maternal investment when reproductive parameters are analyzed (e.g. as in Godfrey et al., 2001).

The present paper is intended as a resource for future studies of primate brain evolution, and has five primary goals. First, we seek to provide a comprehensive and reliable database of endocranial volumes in primate species, with updated alpha taxonomy (Groves, 2005) and male and female data provided separately. These data are tabulated in an electronic appendix listing individual measurements, thus permitting future additions to the present compilation without duplication of data points. Second, we compare endocranial volume between captive and wild conspecifics in order to assess the potential for captive data to influence comparative analyses. Third, we seek to determine whether endocranial volume data should be subjected to an allometric correction formula for calculation of actual brain mass, or whether multiplication of ECV by 1.036 (the density of fresh brain tissue, Stephan, 1960) is sufficient. Fourth, we analyze the allometric relationship between endocranial volume

and body mass in different primate clades, and propose an overall slope for use in comparative studies on brain size variation in primates. Using different parts of our sample, we are able to compare the effects of data quality or quantity on the various methods of analysis. Fifth, we provide an example of an application of these data to a current problem in which data quality is an important issue by testing the maternal energy hypothesis for primate brain evolution (Martin, 1996, 1998; Martin et al., 2005). This hypothesis posits that the brain size of the offspring is constrained by the energy that its mother can provide during early ontogeny (i.e., maternal investment primarily in the form of gestation and lactation).

Methods

Data

Endocranial volumes of primate skulls were measured in eight American and European museum collections (AIMUZ, AMNH, BMNH, DUPC, FMNH, MCZ, UT, USNM, see Electronic Appendix A1 for abbreviations and Appendix B for data). Subsets of these measurements have been published previously as species mean values (Martin, 1990; Kirk, 2006), and others are listed in the PhD thesis of Miller (1997). In addition, we have included ECV data measured by Schultz (partly published in Schultz, 1941, 1942, 1958, 1962, 1965). If a specimen was measured by different researchers, the mean value of all measurements was calculated. Occasionally, specimens are misclassified in museum catalogues, and species identification can be a problem if only the skull or the skeleton is preserved. However, for the major part (88.6%) of our sample, the original collecting locality is known. To determine the provenance of specimens, we used the online catalogues of USNM (http://acsmith.si.edu) and MCZ (http://collections.oeb.harvard.edu), the database of AIMUZ, and the published catalogues of BMNH (Napier 1976, 1981, 1985; Jenkins, 1987, 1990).

Additionally, the literature was searched for ECV data measured using a technique similar to those employed here (methodological details listed in the electronic Appendices A2 and A3; Verheyen, 1962; Ikeda and Watanabe, 1966; Hershkovitz, 1970; Elton et al., 2001), or for brain mass data[1] if ECV was not available (four species; Hrdlicka, 1925; Hopf and Claussen, 1970; Bronson, 1981). Data from these additional sources were included in the compilation only if our own data for a given species were insufficient, or if the other source had much larger samples (i.e., more than twice as many individuals). In order to prevent duplication of specimens, data from different sources were pooled only if the included specimens themselves were known to differ between sources, or if the subspecies, provenance, or museum collection were known to differ. We have also listed species for which available data are not yet sufficient to include them in a comparative study, but for which more data might be obtained in the future. For these species, we also note other sources, even if they are more limited.

Measurements of ECV have been variously conducted by filling the braincase with glass beads, seeds or sand and then measuring the volume of the packing material with a graduated cylinder. Two of us (Kirk and Miller), instead of decanting the seeds into measuring cylinders, weighed them and then converted the mass into volume. It might be expected that beads would fill a larger volume in a cylinder than in a rounded space (e.g. a cranial cavity), as the packing of spherules is looser at the surface, and a rounded cavity has a smaller surface/volume ratio than a cylinder. For the range of values studied here, Miller (1997) found that this factor could lead to a difference of about 4%. However, in practice, we did not detect a corresponding bias in species means between authors using the weighing technique (Kirk,

[1] Due to methodological uncertainties of brain mass measurements, we did not convert brain mass data into ECV by dividing by 1.036g/cc.

Miller) and those using measuring cylinders (Isler, Martin, Schultz, Verheyen, Elton, etc.), and we therefore did not apply a correction formula.

The total number of primate species recognized has more than doubled from 185 in Napier and Napier (1967) to 376 in Groves (2005). We thus follow the taxonomy of Groves (2005, differing from Groves 2001 primarily through a net increase of 20 species) for classification and species definitions. However, in common with many textbooks (e.g. Fleagle, 1999; Cachel, 2006), we reserve the name “Hominidae” for the human lineage and use the family name “Pongidae” for all great apes. Due to the limited number of available specimens, data from separate species were averaged for two genera included in our analyses: *Pygathrix* (comprising *P. nemaeus* and *P. nigripes*) and *Brachyteles* (comprising *B. arachnoides* and *B. hypoxanthus*).

Female, male, and species mean ECV and body mass data are listed in Appendix C. Because sexual dimorphism in body mass is common among anthropoids, mean values for species were calculated as the average of male and female means. We used a minimum of two male and two female individuals to calculate a species mean for anthropoids. For prosimians (Strepsirrhini + tarsiers), a different approach was taken. Because sex was not recorded for numerous individuals in many prosimian species, averaging of mean values only for individuals of known sex would have led to a drastic reduction in sample size. As sexual dimorphism in body size is generally very limited or absent among prosimians (Smith and Jungers, 1997), mean values were calculated for all individuals of a given prosimian species regardless of sex. Here, a minimum of four individuals was considered a sufficient sample size for prosimians.

Body mass data from museum records for the measured crania were used only if known for a majority of the specimens of a given species. As the majority of specimens (88%)

were collected in the wild, these data are not biased by captivity effects. Otherwise, the body mass compilations of Smith and Jungers (1997) and Gordon (2006) were used in our analyses. These data sets were supplemented with additional measurements taken from Thalmann and Geissmann (2000), Araujo et al. (2000), Schuelke et al. (2004) and J. Pastorini (pers. comm.). Details are explained in Appendix A4.

To compare ECV with actual brain mass values, we used the dataset of Stephan, Bauchot and colleagues (Bauchot and Stephan, 1966, 1969; Stephan et al., 1970; Stephan et al., 1981), with several additions (H. Frahm, pers. comm. to R. Deaner) as described in Deaner and Nunn (1999). However, in addition to the brain mass values that were measured by these authors following a strict protocol, the compilations of Stephan and colleagues also include some values from published studies that may represent endocranial volumes (such as Schultz, 1941, 1962) as well as brain mass values that may have been influenced by different preservation techniques (such as Hrdlicka, 1925; Crile and Quiring, 1940; Kennard and Willner, 1941a, b, c). Some of these latter values were derived from individuals that were obviously in very poor physical condition, and the selection criteria of Stephan and colleagues are not explicitly stated.

Statistical analyses

All statistical analyses were performed on $\log_e$ transformed variables, using JMP^{TM} 6.0. A list of taxa included in each analysis is given in Appendix A5. Reduced major axis regressions (RMA) were used to assess the allometric relationship between ln brain mass and ln ECV. To test the suitability of using a simple correction factor to predict brain mass from ECV (i.e., 1.036 for the density of fresh brain tissue), a least-squares regression was calculated with a fixed slope of 1 and the y-intercept was examined. To make predictions, however, the logged species means must be back-transformed, introducing possible transformation bias (Smith, 1993). To estimate transformation bias, the quasi-maximum

likelihood estimator (QMLE) was calculated from the root of the mean square error (RMSE): QMLE = exp($RMSE^2$/2). As QMLE is known for overestimation (Smith, 1993), it can be used as an upper limit for possible transformation bias. Differences in ECV between wild-caught and captive specimens were assessed using unpaired t-tests.

To describe the relationship between ECV and body mass, we applied four line-fitting techniques to our data using species means as well as mean values calculated for females only. These line-fitting techniques include (1) least-squares (LS) regression, (2) major axis (MA, orthogonal) regression (as recommended in Martin and Barbour, 1989), (3) reduced major axis (RMA) regression, and (4) a robust, nonparametric line-fitting method (rotation method, or ROT, Isler et al., 2002)[2]. To test for potential grade shifts within primates, we also examined the independent scaling of ECV within the following groups: (1) hominoids, (2) colobines, (3) cercopithecines, (4) callitrichines, (5) non-callitrichine platyrrhines, and (6) prosimians. ANCOVA was performed with ECV as response and body mass, group, and the interaction between body mass and group as factors. As the interaction term was not significant (p=0.117), the model was recalculated with the factors body mass and group only. Least-squares means permit the evaluation of within-group means adjusted for other effects in the model. Thus, pairwise differences between groups were tested by the Tukey-Kramer HSD test on the least-squares means (Kramer, 1956), which is more conservative than Student's *t*-tests for individual pairwise comparisons.

In addition to our analyses of mean data for species and females, we also examined the relationship between ECV and body mass using phylogenetically adjusted data. A composite supertree including branch length estimations was constructed from Bininda-

[2] Albrecht, Gelvin, and Miller (e.g. Albrecht and Gelvin, 1987; Gelvin and Albrecht, 1987; Gelvin et al., 2000) discuss alternative views regarding allometric approaches and interpretations.

Emonds et al. (2007), complemented with data from Cortes-Ortiz et al. (2003, *Alouatta*) and Newman et al. (2004, *Papio*). The tree in Nexus format is given in Appendix A6. To test whether phylogenetic effects are present in our data, we used Pagel's software CONTINUOUS (Pagel, 1994). The maximum likelihood estimation of Lambda, which measures the degree to which the phylogeny predicts the pattern of covariance among species (Pagel, 1999), was 0.999 (not significantly different from 1), indicating that potential phylogenetic effects might be present in the dataset. We therefore conducted an analysis using phylogenetically independent contrasts, as originally proposed by Felsenstein (1985). Contrasts were generated using the PDAP:PDTree package (Garland et al., 1992) of the Mesquite computer program (Maddison and Maddison, 2005). The appropriateness of branch length estimations was then tested using CONTINUOUS (Pagel, 1994). The maximum likelihood estimation of Kappa, which differentially stretches or compresses individual phylogenetic branch lengths (Pagel, 1997), was 0.905 (95% confidence interval 0.776 – 1.043), justifying the use of our molecular branch length estimations. The likelihood ratio test revealed that the Null hypothesis of equal branch lengths should be rejected (*ln*-likelihood ratio = 75.09, df = 1, p = <0.0001). Independent contrasts were analyzed using least-squares regressions constrained to pass through the origin (Garland et al., 1992).

To test whether changes in ECV lag behind changes in body mass in an evolutionary timescale, we followed the method of Deaner and Nunn (1999). This technique is based on the assumption that, if a lag exists, there should be a positive correlation between the residuals of ECV vs. body mass contrasts (positivized on body mass contrasts) and divergence time. Deaner and Nunn (1999) used brain mass data from Stephan et al. (1981) and pairwise contrasts between extant species, pairing successively the most closely related species that had not been paired previously. However, depending on the details of the phylogenetic tree used, this procedure yields an arbitrary number of pairings between very

distantly related species (e.g. *Colobus badius* vs. *Leontopithecus rosalia* in their analysis of females, or *Miopithecus talapoin* vs. *Tarsius bancanus* in their analysis of males). If present, such pairings with a very ancient divergence time exert a strong influence on the correlation that is to be tested. Thus, we used only tip contrasts (i.e., primarily those between the most closely related species of a genus) for our analysis. To prevent bias from body mass dimorphism in this analysis of evolutionary lag, we used adult female ECV and body mass values.

The maternal energy hypothesis (Martin, 1996, 1998; Martin et al., 2005) predicts that neonatal brain mass should be positively correlated with both maternal basal metabolic rate and gestation length. Basal metabolic rate (BMR) is defined as the metabolic rate of inactive, post-absorptive, adult, non-reproductive animals in a thermoneutral setting. However, in published compilations such as Lovegrove (2000) or White and Seymour (2003), data derived from juveniles have often been included without comment. Some compilations of mammalian BMR contain data of active or anaesthesized animals, or species that have been inadvertently duplicated. Moreover, some viable data were not included in previous compilations, and additional data have since become available (see Appendix A7 for details). Therefore, we reviewed the original literature on primate basal metabolic rates (BMR) and found data for 30 primate species from adult, post-absorptive, non-reproductive, resting or sleeping individuals in their thermoneutral zone. Gestation and lactation lengths for 27 of these species were taken primarily from the compilation of Martin (2007) and other published sources. Values and sources of BMR, gestation and lactation length are listed in Appendix D.

Because data on neonatal brain size are scarce and the relationship between neonatal ECV and adult female ECV does not differ significantly from isometry (reduced major axis regression slope = 1.011, 95% confidence interval 0.953-1.072, r^2 = 0.984, N=22, data from Pagel and Harvey, 1990, and Sacher and Staffeldt, 1974, see also Martin, 1981), we used

adult female brain size as a proxy for neonatal brain size. First, we tested for a positive correlation between BMR and brain size in primates. Such a correlation would indicate a link between energy turnover during rest and the high energetic needs of brain tissue (Armstrong, 1983; Hofman, 1983). Second, we tested whether, in a multivariate model, both BMR and the duration of gestation are positively correlated with brain size. To control for the effects of body mass, we calculated the residuals for of multiple dependent variables from least-squares regressions on body mass. These variables include female mean ECV, gestation length, and basal metabolic rate. To take the effect of body mass into account, it is not feasible to simply include it as an effect in a multiple regression, because the individuals that were used for BMR measurements often do not exhibit a body mass close to species mean body mass. Therefore, we performed regressions of female mean ECV and gestation length using female mean body mass (Appendix C), and the regression of BMR was calculated using the body mass reported for the individuals tested (Appendix D). These residuals were then used to calculate a multiple regression, with residual ECV as the response and residual BMR and gestation length as effects. An analogous analysis was performed for lactation length. The same procedure was also performed using independent contrasts, for which regressions were forced through the origin.

Results

We compiled endocranial volumes (ECV) for 3813 adult specimens from 232 non-human primate species of 67 genera. This sample includes 1935 males (50.7%), 1748 females (45.8%), and 130 (3.4%) individuals of unknown sex. A total of 3363 (88.2%) individuals were wild-caught with known provenance, 305 (8%) were born or died in captivity, and 145 (3.8%) are of unknown provenance. For 2042 (53.6%) specimens, body mass

information was available from museum catalogues or field notes. A complete list of individual endocranial volume (ECV) measurements and matching body mass data is given in Electronic Appendix B, sorted by genus and species names. Together with published records, reliable data on both ECV and body mass are available for 176 species (including at least four individuals per species, two males and two females in anthropoids). Appendix C lists summary data such as species, male and female means, and body mass data.

A) Relationship between endocranial volume and brain mass

For 62 species, both ECV data from this study and brain mass data from the compilations of Stephan and colleagues are available. The relationship between ln ECV and ln brain mass in primates is indistinguishable from isometry at a significance level of 0.05 (reduced major axis: ln brain mass = 0.994 ln ECV + 0.052, 95% confidence interval 0.975-1.012; Table 1). This result is consistent regardless of whether species means are used, or whether mean values for males and females are considered separately. A least-squares regression with a fixed slope of 1 yields an intercept of 0.029 with $\log_e$ transformed data (0.039 and 0.031 for females and males, respectively). Given the isometric relationship between ECV and body mass, this result indicates that the multiplication of ECV (in cc) by the density of fresh brain tissue (1.036g/cc) is appropriate for estimating brain mass (in g). Transformation bias is below 0.7% for all three regressions, and can thus be neglected for practical purposes.

B) Differences in endocranial volumes between captive and wild animals

Our compilation contains ECV data for both wild and captive specimens (≥3 individuals each) of 17 groups (either species means, or sex-specific means in dimorphic species, Table 2). Significant differences in ECV between captive and wild individuals are found in 2 of the 17 groups we examined. However, these two groups do not exhibit the same pattern of variation.

Wild-caught *Callithrix penicillata* have larger endocranial volumes than a group of conspecifics that died in captivity, during transport from Rio de Janeiro to Rotterdam. A similar effect is observed in *Cheirogaleus major*, although it is not significant. By contrast, captive-bred *Otolemur garnettii* have larger endocranial volumes than their wild relatives. In most other groups (11 out of 15), captives have slightly larger ECVs than wild specimens, but the effect comes close to significance only in *Arctocebus calabarensis* and *Pan troglodytes* males.

Bronson (1981) published brain mass and body mass data for 12 species of captive primates, with large sample sizes for each species (between 14 and 260 individuals per species, mean N=76). These data are compared to our ECV values and species mean body mass data (derived predominantly from wild specimens) in Figure 1. This bivariate plot demonstrates that brain mass (in g) is similar to ECV (in cc) for every species (paired *t*-test, *df*=9, p=0.932), whereas body mass is heavily influenced by captivity (paired *t*-test, *df*=11, p<0.0001). The captive primates from Bronson's study are consistently about 33% lighter than their wild conspecifics. This result is found for males and females alike (not shown).

C) Allometric relationship between ECV and body mass

All of the line-fitting techniques used here demonstrate that ECV is negatively allometric with respect to body mass (Table 3). Regression lines fitted to species means across all primates yield remarkably similar results, with slopes ranging from 0.77 (LS) to 0.79 (MA and RMA). Only the 95% confidence limits of the LS-regression include the value of 0.75. When species means for anthropoids are calculated using data for females only, the slopes of all regressions increase slightly (LS: 0.80, MA, RMA and ROT: 0.82). On the other hand, we found a much shallower slope of 0.57 using independent contrasts analysis of ECV vs. body mass (LS regression forced through the origin). However, the slope of the regression using independent contrasts is strongly influenced by the branch length estimations. A punctuational

model of evolution (using equal branch lengths between all nodes) yields a slope of 0.646, in which the contrast between Tarsiiformes and Anthropoidea exerts a strong influence (slope = 0.614 if this contrast is excluded). In this model, deeper contrasts have more influence than if branch lengths are determined by molecular estimates. To further understand why the slope of ECV vs. body mass is so much lower in independent contrasts analysis than in raw data analysis, we analysed the contrasts of superficial and deeper nodes separately (Table 4). In fact, the slope was found to be 0.679 if only deep contrasts were included, but 0.412 if only contrasts within genera were included.

To assess the influence of data quality and quantity on the outcome of independent contrasts analyses, we separately analyzed two subsamples from our dataset. The first subsample is a high-quality dataset (N=50 species, see Figure 2), which includes only the species with the largest sample sizes per genus, and then only if at least 10 individuals were measured (5 males and 5 females in anthropoids). The second subsample is a lower-quality dataset (N=50 species), which includes only the species with the smallest sample size per genus. For both subsamples, LS regressions for ECV vs. body mass using logged species means have steeper slopes than regressions using independent contrasts (Table 4). However, compared to the drastic reduction in slope found for the complete dataset (N=176 species, from 0.773 [raw] to 0.565 [IC]), the reduction is much less pronounced in both the high-quality dataset (from 0.768 [raw] to 0.670 [IC]) and in the low-quality dataset (from 0.773 [raw] to 0.658 [IC]). These analyses suggest that the independent contrasts slope depends primarily on the number of species included, because this factor determines the proportion of within-genus vs. between-genera contrasts.

To examine the influence of grade differences on the relationship between ECV and body mass in primates, we performed an ANCOVA on the raw, logged species means for the following groups: prosimians (lemurs, lorises and tarsiers), cercopithecines, colobines,

hominoids, callitrichines, and non-callitrichine platyrrhines (Table 5, illustrated in Figures 3 and 4). As the interaction term between group and body mass is not a significant effect on ECV, it is possible to fit a common slope between ECV and body mass for all groups. The value of this common slope is 0.646±0.016 (mean±s.e.). For the least-squares mean, hominoids exhibit the highest y-intercept, followed (successively) by cercopithecines, non-callitrichine platyrrhines, colobines, callitrichines, and prosimians. The Tukey-Kramer HSD test yields three different grades. The grade with the largest relative ECVs includes hominoids, cercopithecines, and non-callitrichine platyrrhines. A second grade with intermediate relative ECV sizes includes colobines and callitrichines. Finally, the prosimians constitute a third grade with the smallest relative ECV sizes. The same grades are also found if only female values are analysed (N=166).

Prosimians are similar in having relatively small brain sizes compared to anthropoids (Figure 3). Indeed, some nocturnal lemurs, including *Cheirogaleus, Avahi* and *Lepilemur*, have the smallest relative brain sizes of any primate. By contrast, the large diurnal and cathemeral Lemuridae are comparatively highly encephalized, and exceed Lorisiformes in relative brain size. Although prosimians as a group comprise a grade with lower encephalization than anthropoids, *Daubentonia* is remarkable in demonstrating a very large brain relative to body size.

Within New World monkeys, there are major intergeneric differences in relative brain size that do not coincide with higher-level phylogenetic relationships (Figure 4). Callitrichines, *Aotus* and *Callicebus* clearly belong to the same relatively small-brained grade, whereas *Cebus*, *Saimiri* and some members of Pitheciidae (*Chiropotes*, *Cacajao*) are highly encephalized. *Alouatta* also has a relatively much smaller brain than other atelines (*Ateles*, *Brachyteles*, and *Lagothrix*).

Within the Catarrhini, colobines have smaller brains than cercopithecines and hominoids and exhibit a more negative allometric relationship between ECV and body mass than all other groups (Table 6, Figure 3). Furthermore, non-human hominoids have larger relative brain sizes than cercopithecines (ANCOVA, N=55, $p<0.0001$). This difference between hominoids and cercopithecines is also statistically significant if the analysis is restricted to adult female values only ($p=0.007$). Within both cercopithecoids and hominoids, slopes for females are steeper than slopes for males, particularly in colobine monkeys (Table 6).

To detect a possible lag in brain size changes as opposed to changes in body mass, we looked for a positive correlation between the residuals of ECV contrasts vs. body mass contrasts (positivized on body mass contrasts) and time of divergence, using only tip contrasts of adult female means (N=53). However, no significant correlation was found and thus no evolutionary lag in ECV was detected. Similar results were also found when each of the major taxonomic groups was tested separately.

Within species, the slope of the LS regression of ECV and body mass is much lower than that found between species (Table 7). Species with marked sexual dimorphism (i.e., those with a male/female ratio > 1.2) exhibit a steeper slope than monomorphic species (i.e., male/female ratio < 1.1; unpaired t-test: df=25, $p=0.007$, means of slope 0.239 vs. 0.153).

D) Maternal energy hypothesis

In this analysis, ECV means from adult females were used for anthropoids, and species mean ECVs were used for prosimians. We found that BMR is positively correlated with ECV in primates after controlling for the effect of body mass, both in raw species data (N=30) and after calculating independent contrasts (Figure 5). In a multiple regression of residuals relative to body mass (Table 8), both BMR and gestation length are positively

related to ECV (N=27). Lactation length, on the other hand, is not significantly correlated to ECV, if BMR is included in the analysis (N=27).

Discussion

A) Relationship between endocranial volume and brain mass

The relationship between ECV and brain mass in primates is indistinguishable from isometry at a significance level of 0.05. This result is consistent whether species means are used, or whether mean values for males and females are considered separately. Although we would expect ECV to be greater than brain mass due to the added volume of the meningeal membranes, blood vessels, and the subarachnoid space, our analysis demonstrates that brain mass (in g) is approximately 4% larger than ECV (in cc). We therefore conclude that the correction formula of Brain Mass = ECV*1.036g/cc (the density of fresh brain tissue, Stephan, 1960) would be sufficient for comparative analyses, and may even be unnecessary given the uncertainties of brain mass recordings. Because brain mass is influenced by preservation techniques (e.g., storage in formalin increases apparent brain mass, whereas alcohol decreases apparent brain mass; Bauchot and Stephan, 1969), ECV might provide a more reliable estimate of the actual brain size of an individual during its lifetime. This conclusion is probably most applicable for species from the same mammalian order, in which the cranial cavity is filled to a similar extent by brain tissue.

B) Differences in ECV between captive and wild animals

The data presented in Table 2 strongly suggest that captivity has a minimal influence on endocranial volume in primates. In 12 out of 17 taxa, captives had slightly larger ECVs

than wild specimens, but the effect was significant only in *Otolemur garnettii*. Because the matching body masses are unknown in most cases, these results could be explained by the larger total body size that captive bred individuals typically attain under good conditions. In any event, we found no evidence for a general trend towards brain size reduction indicating a "domestication effect" in captive primates, as has been found in other mammals that have been domesticated for extended periods (e.g. Kruska, 1987). Indeed, brain size seems to be much more stable under different nutritional conditions than body mass, and could hence be used as a more reliable indicator of species size than body mass. However, this is only advisable if body mass data for wild populations is scarce and if there is no reason to suspect that the species differs in relative brain size from it's closest relatives.

These conclusions are supported by the comparisons between our predominantly wild ECV data and captive brain mass values from Bronson (1981) (Figure 2). While brain mass (in g) is not significantly different from ECV (in cc) for each of the 12 species in Bronson's study, the captive primates in Bronson's sample are consistently about 33% lighter than their wild conspecifics.[3] Thus, brain mass values from these captive specimens could be included in comparative studies, provided that they were matched with wild body mass averages. If the body mass data from captivity were to be used, this procedure would result in serious overestimation of the degree of encephalization in Bronson's captive primate sample.

C) Allometric relationship between ECV and body mass

Across all primates, ECV is negatively allometric with respect to body mass. Overall, best-fit lines of ln ECV on ln body mass have slopes between 0.77 and 0.82, with minor

[3] This finding is in contrast to Smith and Jungers results on primate body mass data, where captives are consistently heavier on average than wild-caught individuals. Most likely, captives from laboratories are rather immature (though dentally adult) and may suffer from health problems, whereas captives from zoos tend to be overweight.

variation depending on the line-fitting method used (Table 3). This result is similar to that obtained in previous analyses, including those of Harvey and Clutton-Brock (1985; N= 107, slope of LS-regression = 0.776, r^2 = 0.918) and Stephan and colleagues (1981; N=80, slope of LS-regression = 0.752, r^2 = 0.943). Furthermore, the r^2 value for our dataset is slightly higher than those of most previous studies of brain-body allometry (0.948 as compared to 0.943 in Stephan et al. [1981], and 0.918 in Harvey and Clutton-Brock [1985]). The slope of the independent contrasts analysis (IC) of ECV vs. body mass varies according to the branch lengths that are used, and is estimated here as 0.58. This slope is similar to the value 0.56 that Dubois (1897) derived from comparing pairs of species within a number of mammalian orders. However, if only deep contrasts are included, the slope is 0.67. All comparative phylogenetic methods force us to balance the influence of deeper and more superficial contrasts through the choice of branch length estimations.

From analyses of different subsets of our data, we conclude that both the inclusion of more species and lower data quality lead to a decrease of the slope of the regression line in independent contrasts analysis. Whereas the slope of the species means regressions remain stable when data subsets of varying quality are analysed, the slope of the independent contrasts regression is seriously affected by both data quality and quantity as predicted by Martin et al. (2005) (Table 4). The complete dataset of 176 species shows a greater reduction in slope following contrast analysis than either the high-quality or the low-quality dataset (50 species each). A likely explanation for this result might be that the complete dataset has a higher proportion of within-genus contrasts relative to the number of between-genera contrasts. Furthermore, for closely related species pairs with similar body masses and ECVs, the error term will be greatly exaggerated when contrasts are calculated.

Still, the discrepancy between the slopes obtained from raw data and from independent contrasts analyses is pronounced. Not surprisingly, ANCOVA reveals that the overall

relationship between ECV and body mass in primates is strongly influenced by the presence of grade shifts between taxonomic groups. All of the major groups considered in this analysis have a relationship between ln ECV and ln body mass that is well-described by a regression line with a slope of 0.646. If a line with this common slope is fitted to the logged species means of the complete data set, it becomes clear that all relatively large-bodied extant primates are also relatively large-brained. This finding may be connected with the results of Deaner et al. (2007), who report that absolute brain size is the best predictor of domain general intelligence in primates.

Regardless of which line-fitting technique is used to compare across taxa, some primate species are clearly outliers from their close phyletic relatives in terms of relative ECV. *Daubentonia* is the most salient outlier within strepsirrhines (as already reported by Stephan et al., 1981; see also Martin, 1990; Kaufman et al., 2005), with a brain as large as a monkey of equivalent body size (Figure 3). Gibson (1986) and Sterling (1994) have suggested that the high degree of encephalization seen in *Daubentonia* could be related to its complex foraging behaviors and associated sensorimotor abilities. Indeed, the aye-aye exhibits a relatively large frontal cortex for its brain size (Bush and Allman, 2004), and olfactory and auditory structures are enlarged (Kaufman et al., 2005). Among cercopithecines, *Miopithecus* has a relatively small brain (see Figure 3). This finding is contrary to the result obtained by Bauchot and Stephan (1969) using a regression line fit to all primates. *Macaca sylvanus* is also a prominent outlier, as it has a brain that is only the size of a colobine of equivalent body mass. However, the species mean ECV for *M. sylvanus* is derived from relatively few individuals, whereas body mass estimates are more reliable. If the small ECV of *M. sylvanus* can be confirmed by a larger sample, this finding may hint at a serious energy constraint in this monkey species, which commonly lives in harsh, seasonal montane habitats (Modolo et al., 2005).

Despite the existence of such outliers, our results indicate that living primates can be broadly divided into three groups on the basis of relative ECV. Prosimians as a group typically have smaller relative brain sizes than anthropoids. Within anthropoids, colobines and some platyrrhines (including the callitrichines, *Aotus*, *Callicebus*, and *Alouatta*) have smaller relative brain sizes than hominoids, cercopithecines, pitheciines, most atelines, *Cebus*, and *Saimiri*. These findings provide further evidence that relative brain size increased during the course of anthropoid evolution (Martin, 1990; Kirk, 2006). Whether such increases occurred independently in catarrhines and platyrrhines is not immediately clear based on this analysis. Furthermore, within catarrhines, our data suggest that relative brain size either increased independently in both hominoids and cercopithecoids, or that relative brain size decreased in colobines.

In both cercopithecoids and hominoids, slopes for females in regressions of ECV on body mass are steeper than slopes for males, particularly in colobine monkeys (Table 6). In these groups, sexual dimorphism in body mass is more pronounced in larger species (as in many mammals, Rensch's rule, Rensch, 1950, 1959). This finding indicates that especially large-bodied catarrhine males are less encephalized than females of the same species. One interpretation of this finding is that, in these highly dimorphic species, the body mass of one or the other sex changed without an equivalent change in brain size. However, brain size does not lag behind body size changes between closely related species (Deaner and Nunn, 1999). We tested our data with the same technique as that used by Deaner and Nunn (1999), and we were also unable to detect any lag. However, this result does not rule out the possibility of an intraspecific lag effect.

We conclude that, for some comparative purposes, it may be generally preferable to use only female data on brain and body size, especially for dimorphic species. In addition to this practical indication that use of female values may be the optimal method for excluding

effects of sexual dimorphism, there are some contexts in which maternal body mass is the appropriate variable in any case.

D) Testing the maternal energy hypothesis in primates

Martin (1996, 1998) reported that analyses of residual values and partial correlations revealed that body size, BMR and gestation period are all associated with brain size in placental mammals. In an independent study of primate genera alone, Little (1989) used path analysis to infer that gestation period and metabolic rate are both related to brain size. However, the proposed connection between BMR and brain size has been challenged by certain authors. McNab and Eisenberg (1989) found no significant relationship between residuals for BMR and brain size for placental mammal species (n = 172). However, their analysis was statistically flawed and a weakly significant correlation was in fact present in their data (Martin, 1998). It has now emerged that the dataset used by McNab and Eisenberg (1989) was itself afflicted by a serious error. The data on rodent brain sizes, taken from Mace et al. (1981) and accounting for 40% of the dataset, were systematically biased by accidental addition of an increment to the brain mass of every species (Isler and van Schaik, 2006). A different challenge to the results reported by Martin (1996) was that they may have been biased by phylogenetic inertia. Following analyses using independent contrasts, it was reported that there is no significant relationship between BMR and adult brain size for mammals generally (Pagel and Harvey, 1988a), although a significant relationship between gestation period and neonatal brain size did remain (Pagel and Harvey, 1988b)[4]. Barton (1999) later reported that for primates no significant correlation between adult brain size and

[4] The maternal energy hypothesis specifically predicts that gestation period should be better correlated with neonatal brain size than with adult brain size. However, because of insufficient data for neonatal brain size, adult female brain size is typically used as a proxy.

BMR or gestation period remains after analysis using independent contrasts. However, it had been shown for a sample of 51 placental mammal species that significant correlations between adult brain size and both BMR and gestation persist even after calculation of independent contrasts (Martin, 1998).

Here, using a new compilation of primate BMR data following strict criteria (Appendix D), we find that BMR is significantly correlated with ECV in primates after controlling for the effect of body mass and phylogeny (N=30 species, Figure 5). This result confirms the findings of Isler and van Schaik (2006), which were obtained using a smaller and less representative dataset (N=23 species). In a multiple regression (Table 8), both BMR and gestation length are positively related to ECV (N=27 species). The present dataset is heavily biased towards small species (strepsirrhines and callitrichines), so brain size is linked to bodily energetics even in these relatively small-brained primates. The results reported here show that use of high-quality data (minimizing the error terms that are unfortunately exaggerated by calculation of independent contrasts) in fact permits reliable identification of significant correlations linking both BMR and gestation period to adult brain size in primates.

Conclusions

By compiling endocranial volume data (ECV) from 3813 primates, at least 89% of which were wild-caught, we have shown that:

1) ECV scales isometrically with respect to brain mass in primates, confirming the result obtained by Martin (1990) using a much smaller dataset. ECV should be multiplied by 1.036g/cc (the density of fresh brain tissue) to obtain brain mass.

2) In general, ECV does not differ between captive and wild animals, whereas body mass may vary tremendously according to living and rearing conditions. We conclude that

ECV data from a large sample of wild or captive specimens in combination with body mass data from wild-caught animals provide the most reliable basis for comparative analyses.

3) ECV is negatively allometric with respect to body mass in primates. This scaling relationship is strongly influenced by the presence of grade shifts, and a regression line with a slope of 0.646 generally describes brain-body allometry within major taxonomic groups. Using this criterion, all relatively large-bodied extant primates are also relatively large-brained.

4) Using the ECV compilation and new and revised data on the basal metabolic rate of primates, we add support to the maternal energy hypothesis (Martin, 1996, 1998; Martin et al., 2005) by showing that both BMR and gestation length are positively correlated with brain size, controlling for body mass, even after the application of the method of independent contrasts. However, to test the effect of maternal energy investment more precisely, more data on primate neonatal brain size are urgently needed.

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Figure Legends

Figure 1: Brain mass data from Bronson (1981) (circles) compared to ECV species averages from this study (triangles). The line represents the least-squares regression of ECV vs body mass for the 176 primate species in our sample.

Figure 2: Contrasts of ln(ECV) vs. contrasts of ln(Body mass), positivized on body mass contrasts, in a high quality dataset. Only the species with the largest sample size per genus are included, and only if at least 10 individuals were measured (at least 5 males and 5 females in the case of anthropoids). The slope of the least-squares regression forced through 0 is 0.670.

Figure 3: ln(ECV) vs. ln(Body mass) in different groups of non-human primates. *Tarsius, Daubentonia, Miopithecus,* and *Macaca sylvanus* are labeled. Regression equations are given in Table 6.

Figure 4: ln(ECV) vs. ln(Body mass) in Platyrrhini. Regression equations are given in Table 6.

Figure 5: ECV Residuals vs. BMR Residuals in primates: a) N=30 species means, slope 0.380, r^2 = 0.350, p = 0.0006; b) N=29 independent contrasts, molecular branch lengths, slope = 0.395, r^2 = 0.226, p=0.006.

Tables

Table 1: Differences between ECV of wild and captive primates in our compilation.

			ECV mean		N		
Species	Sex	p-value	wild	captive	wild	captive	Captives are:
Arctocebus calabarensis	both	0.091	6.77	**7.82**	18	3	captive-bred
Callithrix penicillata	both	**0.001**	**7.66**	6.70	17	12	wild-born?
Cheirogaleus major	both	0.091	**5.90**	5.47	10	3	wild-born?
Eulemur mongoz	both	0.182	18.89	**20.97**	8	3	wild-born
Lemur catta	both	0.545	22.24	**23.34**	6	4	captive-bred
Leontopithecus rosalia	both	0.274	12.48	**13.17**	3	4	captive-bred
Macaca mulatta	female	0.282	81.50	**84.64**	8	50	captive-bred
Macaca mulatta	male	0.282	91.59	**94.60**	13	31	captive-bred
Mandrillus sphinx	male	0.342	159.69	**167.05**	13	3	wild-born?
Otolemur garnettii	both	**0.011**	10.24	**11.54**	15	14	captive-bred
Pan troglodytes	female	0.571	347.15	**354.17**	50	6	wild-born?
Pan troglodytes	male	0.073	381.59	**417.00**	47	5	wild-born?
Papio anubis	male	0.385	**183.00**	177.00	15	3	captive-bred
Saguinus fuscicollis	both	0.413	**8.02**	7.83	22	6	captive-bred
Saimiri sciureus	both	0.438	**24.15**	23.61	88	16	captive-bred
Tarsius syrichta	both	0.321	3.28	**3.51**	6	3	wild-born
Varecia sp.	both	0.323	31.83	**33.01**	10	4	captive-bred

Unpaired t-tests, two-tailed, equal variances. Significant differences and the larger mean are highlighted in bold.

Table 2: Brain mass (data from Stephan and colleagues) vs. endocranial volumes (this study).

					RMA				LS slope=1	
	N	r^2	RMSE	QMLE	intercept	slope	lower CL	upper CL	intercept	p-value
Species means	62	0.995	0.094397	1.0045	0.052	0.994	0.975	1.012	0.029	0.017
Females	60	0.991	0.116442	1.0068	0.060	0.994	0.970	1.019	0.039	0.012
Males	63	0.994	0.101659	1.0052	0.047	0.996	0.976	1.016	0.031	0.018

RMA: reduced major axis regression, LS: least-squares regression, RMSE: root of mean square error, QMLE: quasi-maximum likelihood estimator of transformation bias, CL: confidence limit of slope at alpha=0.05, LS slope=1: least-squares regression with fixed slope = 1. In this analysis, the unusually large brain of "*Tarsius tarsier*" (cf. *T. spectrum*) in the Stephan dataset was omitted. It originates from two laboratory individuals in Kennard and Willner (1941c), and the body mass values reported for this species are also much larger than those in Smith and Jungers (1997). The quasi-maximum likelihood estimator (QMLE, Smith, 1993) was calculated as $\exp(RMSE^2/2)$. Thus, transformation bias is below 0.7% for all three regressions.

Table 3: Best-fit lines for ln(ECV) vs. ln(Body mass) in nonhuman primates

	Logged species means					
	N	r^2	LS-regression	Major axis	Reduced major axis	Rotation line
Species means	176	0.948	0.773 (0.745-0.800)	0.789 (0.761-0.817)	0.793 (0.766-0.822)	0.783
Females in anthropoids, species means in prosimians	170	0.940	0.796 (0.765-0.827)	0.816 (0.784-0.847)	0.821 (0.790-0.853)	0.815
	Independent contrasts					
	N	r^2	LS-regression forced through 0			
Species means	175	0.771	0.565 (0.519-0.611)			
Females in anthropoids, species means in prosimians	169	0.721	0.567 (0.513-0.621)			

Slope and 95% confidence interval of slope are shown.

Table 4: Regression for ln(ECV) vs. ln(Body mass) in different samples of primates

	Species means (LS-regression)			IC (LS-regression through 0)		
	N	slope	r^2	N	slope	r^2
All species means	176	0.773±0.014	0.948	175	0.565±0.023	0.771
High-quality data set	50	0.768±0.024	0.956	49	0.670±0.034	0.880
Low-quality data set	50	0.773±0.027	0.944	49	0.658±0.040	0.834
Tip contrasts (within genus)				110	0.412±0.030	0.629
Deep contrasts				65	0.679±0.030	0.885

Slope: mean ± s.e. Subsamples: The high-quality dataset includes only the species with the largest sample sizes per genus, and then only if at least 10 individuals were measured (5 males and 5 females in anthropoids). The low-quality dataset includes only the species with the smallest sample size per genus.

Table 5: Results of ANCOVA for ECV species means, body mass and group differences (N=176 species)

	Model 1: r^2 = 0.977				Model 2: r^2 = 0.976		
	DF	F	p		DF	F	p
Body mass	1	295.1	<0.0001	Body mass	1	1605	<0.0001
Group	5	31.37	<0.0001	Group	5	39.39	<0.0001
Body mass * group	5	1.791	0.117				
						LS	
				Group	Level	mean	s.e.
				Hominoids	A	3.966	0.0595
				Cercopithecines	A	3.844	0.0329
				Non-callitrichine platyrrhines	A	3.831	0.0318
				Colobines	B	3.581	0.0411
				Callitrichines	B	3.389	0.0592
				Prosimians	C	3.212	0.0375

Tukey-Kramer HSD test: Levels not connected by the same letter are significantly different (alpha = 0.05). The estimate of the effect of body mass in Model 2 is 0.646±0.016 (mean±s.e.).

Table 6: Slopes of east-squares regressions of ln(ECV) vs. ln(Body mass) in different groups of primates

	All			Male			Female		
	slope	r^2	N	slope	r^2	N	slope	r^2	N
All	0.773±0.014	0.948	176	0.754±0.014	0.949	167	0.791±0.016	0.936	166
Prosimians	0.676±0.022	0.955	45	0.690±0.023	0.959	39	0.668±0.025	0.948	41
Callitrichines	0.618±0.059	0.903	14	0.627±0.052	0.930	13	0.616±0.070	0.874	13
Non-callitrichine platyrrhines	0.667±0.063	0.767	36	0.659±0.062	0.768	36	0.654±0.067	0.748	34
Hominoids	0.579±0.026	0.977	14	0.548±0.026	0.973	14	0.640±0.026	0.981	14
Cercopithecines	0.576±0.025	0.930	41	0.532±0.031	0.888	40	0.636±0.025	0.943	40
Colobines	0.435±0.081	0.545	26	0.386±0.076	0.530	25	0.522±0.115	0.483	24

Slope: mean ± s.e.

Table 7: Least-squares regressions for ln(ECV) vs. ln(Body mass) within different primate species (N>17)

	N	Slope: mean±s.e.	r^2	Body mass dimorphism
Alouatta seniculus	31	0.207±0.047	0.401	1.28
Aotus lemurinus	31	-0.122±0.080	0.074	1.05
Cebus apella	41	0.128±0.055	0.124	1.36
Cebus capucinus	23	0.054±0.047	0.059	1.35
Cebus libidinosus	47	0.067±0.044	0.05	1.38
Cebus nigritus	87	0.149±0.036	0.17	1.47
Cebus nigritus X libidinosus	33	0.147±0.073	0.115	1.45
Cercopithecus albogularis	31	0.178±0.052	0.29	1.64
Cercopithecus petaurista	18	0.255±0.074	0.424	1.47
Chlorocebus pygerythrus	60	0.221±0.031	0.464	1.42
Colobus guereza	29	0.318±0.070	0.435	1.29
Galago demidoff	27	0.092±0.079	0.051	1.04
Galago moholi	49	0.063±0.052	0.031	1.02
Galago senegalensis	193	0.123±0.031	0.075	1.07
Hylobates lar	94	0.098±0.051	0.036	1.08
Macaca fascicularis	92	0.184±0.038	0.206	1.42
Macaca mulatta	82	0.215±0.035	0.321	1.40
Macaca nemestrina	20	0.200±0.054	0.433	1.70
Nasalis larvatus	37	0.241±0.027	0.69	1.99
Papio anubis	19	0.307±0.049	0.695	1.73
Perodicticus potto	29	0.072±0.067	0.041	0.92
Pongo pygmaeus	18	0.279±0.068	0.511	2.17

Presbytis melalophos	21	0.160±0.192	0.035	1.00
Presbytis rubicunda	50	0.144±0.102	0.039	1.01
Saguinus fuscicollis	21	0.078±0.081	0.046	1.02
Saguinus oedipus	49	0.238±0.054	0.291	0.94
Saimiri sciureus	76	0.059±0.063	0.012	1.15
Trachypithecus cristatus	25	0.377±0.161	0.193	1.11
Trachypithecus obscurus	28	0.173±0.101	0.102	1.09

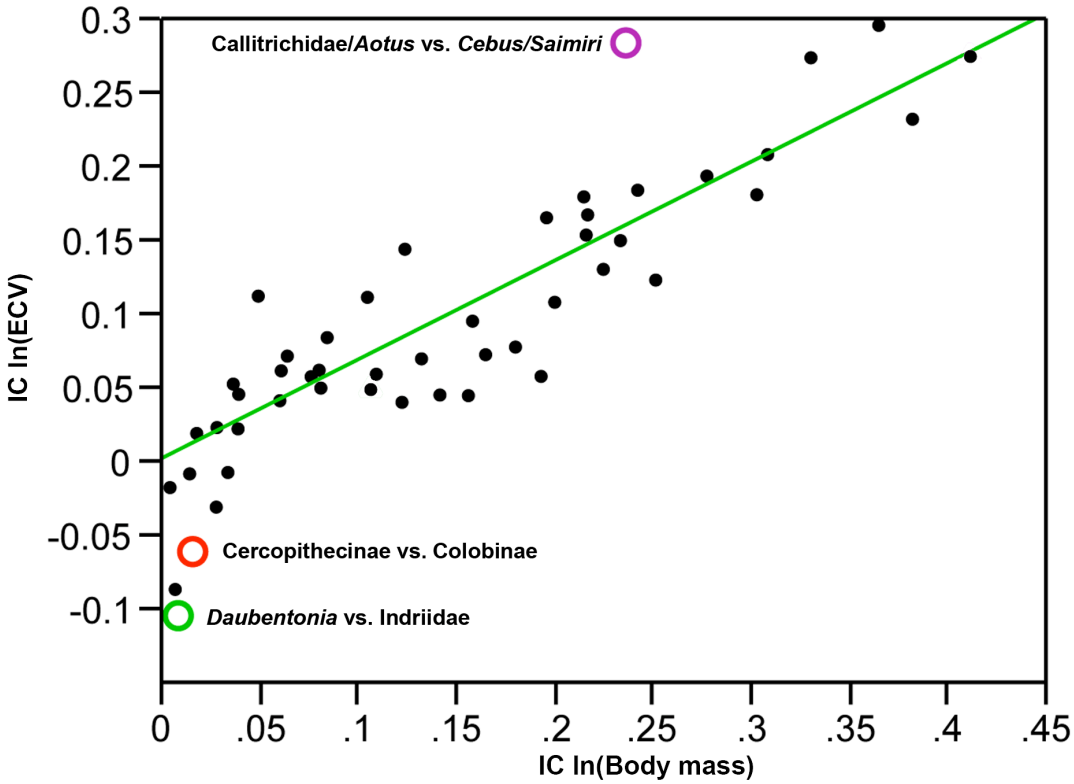
Body mass dimorphism is expressed as the ratio between male and female body mass as recommended by Smith (1999).

Table 8: Test of the maternal energy hypothesis in primates. Multiple regression with residuals of ECV as response, residuals of basal metabolic rate (BMR) and residuals of gestation length or residuals of lactation length as effects.

Multiple regressions							
Response Res ECV		Species means (N=27)			Independent contrasts (N=26)		
	effect	estimate	t-Ratio	p-value	estimate	t-Ratio	p-value
Model 1	Intercept	0.014	0.44	0.666	zeroed		
	Res BMR	0.422	4.35	0.0002	0.461	3.58	0.002
	Res Gestation	0.325	2.45	0.022	0.427	2.22	0.036
Model 2	Intercept	0.014	0.41	0.687	zeroed		
	Res BMR	0.409	3.81	0.001	0.376	2.69	0.013
	Res Lactation	0.134	1.45	0.159	0.140	1.68	0.106
Model 3	Intercept	0.014	0.43	0.671	zeroed		
	Res BMR	0.410	4.03	0.001	0.417	3.04	0.006
	Res Gestation	0.292	1.92	0.067	0.349	1.66	0.111
	Res Lactation	0.047	0.47	0.642	0.082	0.94	0.358
Calculation of residuals		slope: mean±s.e.	intercept	r^2	slope: mean±s.e.	intercept	r^2
ln BMR vs. ln corresponding body mass		0.785±0.043	0.592	0.930	0.746±0.044	zeroed	0.926
ln ECV vs. ln body mass*		0.759±0.030	-2.442	0.962	0.700±0.036	zeroed	0.936
ln gestation vs. ln body mass*		0.101±0.032	4.266	0.286	0.114±0.030	zeroed	0.372
ln lactation vs. ln body mass*		0.422±0.051	2.079	0.736	0.408±0.074	zeroed	0.543

* Female means for anthropoids, species means for prosimians (lorises, lemurs and tarsiers).

Figure 1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0.15
0.1
0.05
0
-0.05
-0.1
IC ln(ECV)
Callitrichidae/*Aotus* vs. *Cebus/Saimiri*
Cercopithecinae vs. Colobinae
Daubentonia vs. Indriidae
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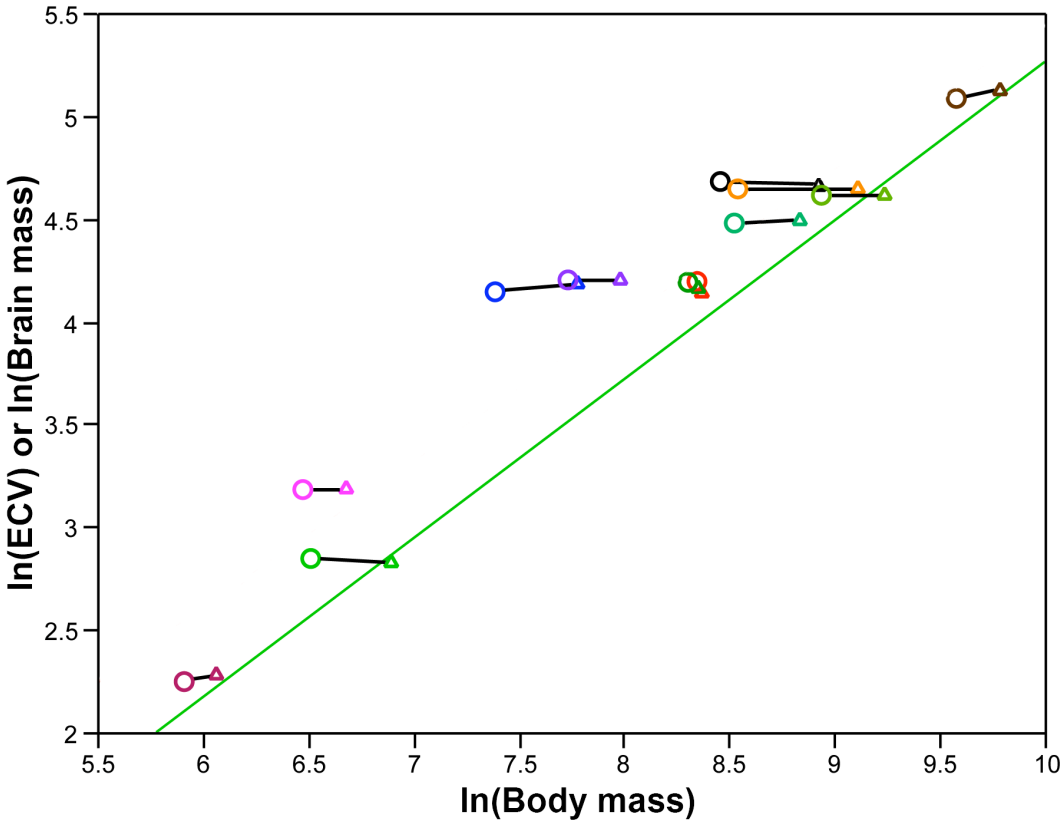
.1
.15
.2
.25
.3
.35
.4
.45
IC ln(Body mass)

Figure 2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5
4.5
4
3.5
3
2.5
2
ln(ECV) or ln(Brain mass)
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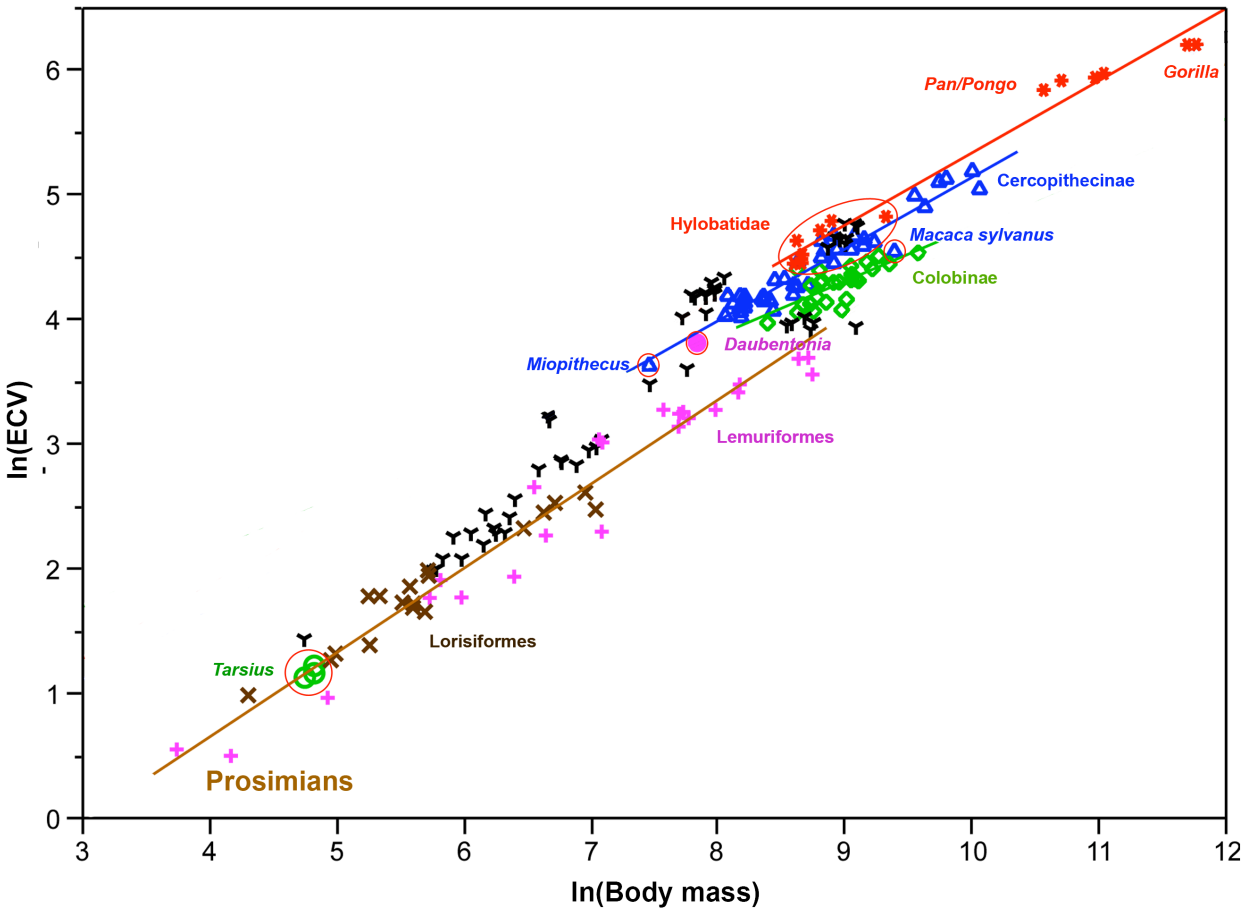
6
6.5
7
7.5
8
8.5
9
9.5
10
ln(Body mass)

Figure 3


ln(ECV)
ln(Body mass)
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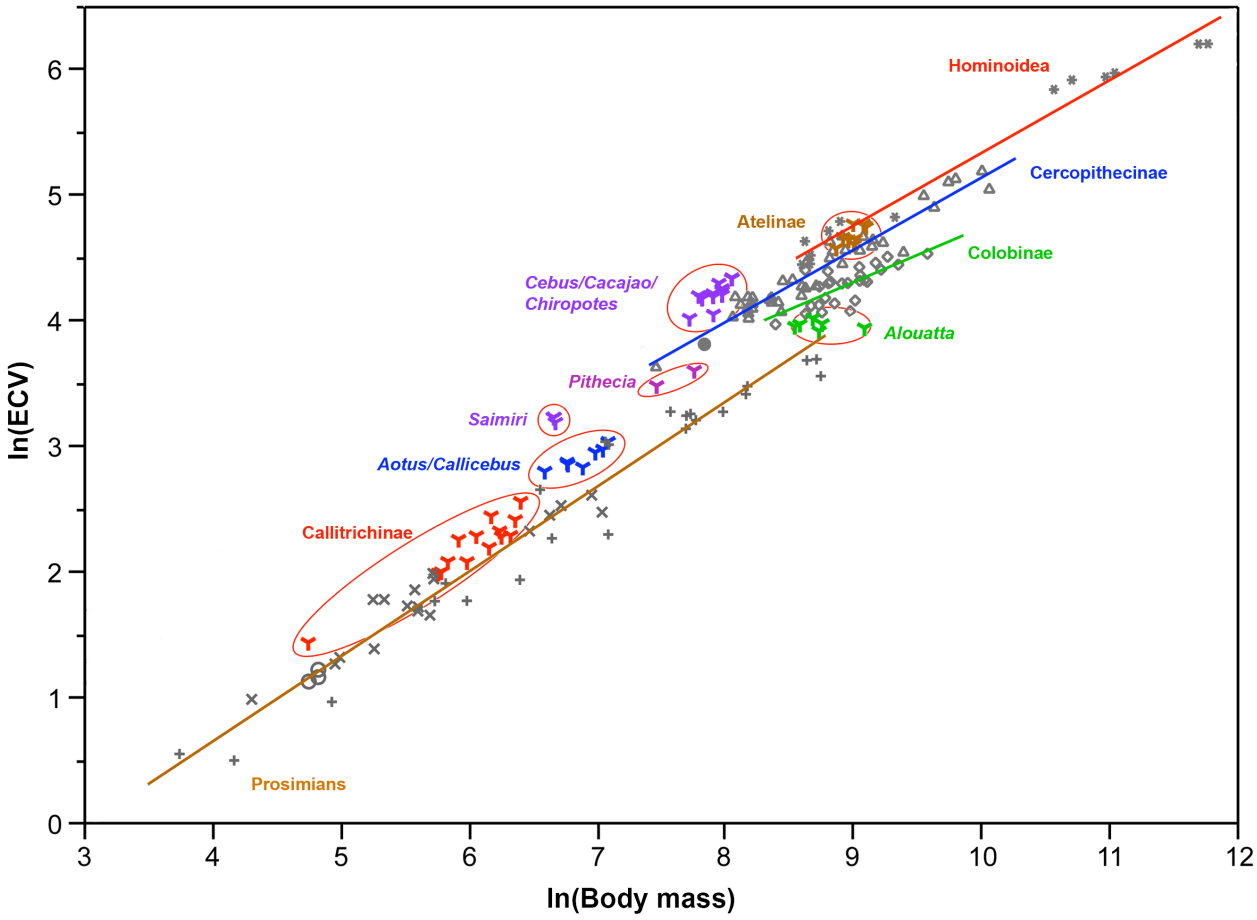
2
3
4
5
6
3
4
5
6
7
8
9
10
11
12
Pan/Pongo
Gorilla
Cercopithecinae
Hylobatidae
Macaca sylvanus
Colobinae
Daubentonia
Miopithecus
Lemuriformes
Lorisiformes
Tarsius
Prosimians

Figure 4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Cercopithecinae
Atelinae
Colobinae
Cebus/Cacajao/
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Alouatta
Pithecia
Saimiri
Aotus/Callicebus
Callitrichinae
Prosimians
ln(ECV)
ln(Body mass)
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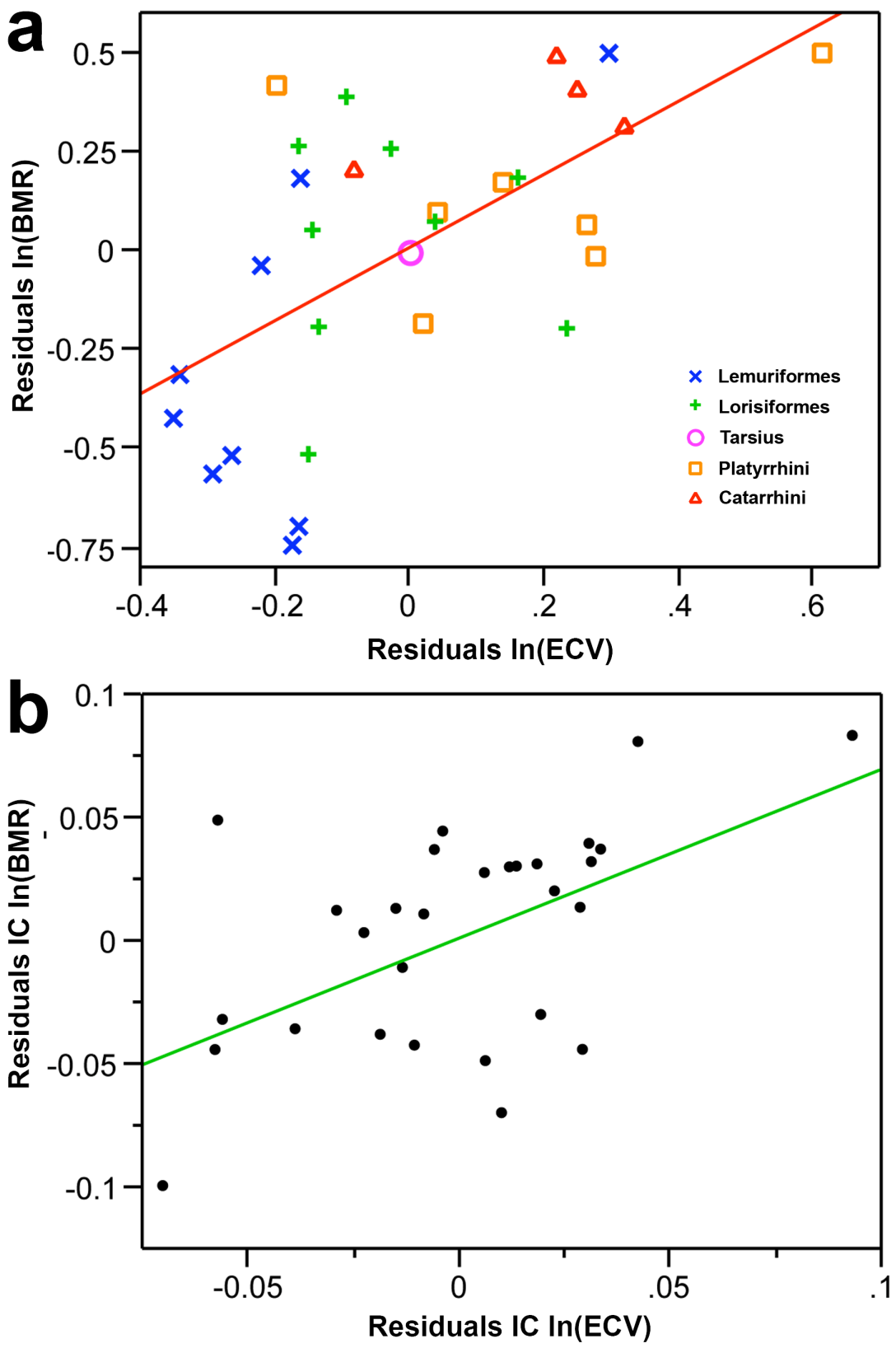
2
3
4
5
6
3
4
5
6
7
8
9
10
11
12

Figure 5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Residuals ln(BMR)
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0
.2
.4
.6
Residuals ln(ECV)
Lemuriformes
Lorisiformes
Tarsius
Platyrrhini
Catarrhini
b
0.1
0.05
0
-0.05
-0.1
Residuals IC ln(BMR)
-0.05
0
.05
.1
Residuals IC ln(ECV)